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REFLECTIONS ON A 1975 EXPEDITION TO THE LOST WORLD OF THE ALAKA‘I AND OTHER NOTES ON THE NATURAL HISTORY, SYSTEMATICS, AND CONSERVATION OF KAUA‘I BIRDS

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ABSTRACT.—We observed, tape recorded, and photographed birds of the Alaka‘i Plateau on Kaua‘i, Hawai‘i for one week during the summer of 1975. We observed all but one of the island’s historically known species and compared the Alaka‘i Plateau with the more accessible Koke‘e area. Ours were the last studies before catastrophic changes in the Kaua‘i avifauna and included many observations that cannot now be repeated. This retrospective report presents our findings in the light of subsequent events. Because our Alaka‘i studies were seminal in the development of the current AOU classification of Hawaiian native passerines, we defend that classification against recent challenges and further refine it. The controversial genus *Hemignathus* is shown to be supported by a suite of synapomorphies of plumage, bill morphology, and vocalizations. We advocate removal of the ‘Anianiau from *Hemignathus* and classify it as *Magumma parva*. Our studies of foraging behavior and vocalizations support the recent recognition of the Kaua‘i ‘Amakihi (*H. kauaiensis*) as a separate species and suggest that the ‘Elepaio (*Chasiempis*) is best split into three species (*sclateri*, *ibidis*, and *sandwichensis*). Major hurricanes in 1983 and 1992 appear to have severely impacted Alaka‘i bird populations with the subsequent extinction of the Kaua‘i ‘O‘o (*Moho braccatus*) and possibly the Kama‘o (*Myadestes myadestinus*), and the island population of ‘O‘u (*Psittirostra psittacea*). We report some of the last natural history observations on these species. Formerly adaptive strategies for storm survival, including taking refuge in valleys, are no longer effective because the lowlands are now infested with mosquito-borne avian diseases. The Puaiohi (*M. palmeri*), a ravine specialist, suffered less from the storms although its population remains perilously low. Other forest birds, especially the ‘Akikiki (*Oreomystis bairdi*), show noticeable declines since 1975. We speculate that introduced organisms such as alien plants can have a deleterious effect on ecosystems by altering feeding methods of birds even in areas where the weeds do not occur. We caution against the overly conservative use of species-level taxa for setting conservation priorities on remote islands. *Received 24 October 1996, accepted 27 June 1997.*

In July 1975 we spent a week in one of Hawai‘i’s last strongholds for native birds, the fabled Alaka‘i Swamp on Kaua‘i. We were

fortunate to find all but one of Kaua‘i’s historically known native bird species. At that time, we assumed that this relatively large wilderness area, under no obvious threat, would remain a refuge for endangered birds at least for the near future. Thus, although our observations contributed to subsequent publications, we published no general summary of our expedition. Time has shown that our optimism was naive; we made some of the last observations and tape recordings, and took some of the last (or only) photographs, of sev-

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eral species, and made the last natural history studies of several others under anything resembling "normal" conditions. We herein report numerous observations that will likely never be repeated and make comparisons with the current status of birds on Kaua'i. We interpret and amplify our 1975 observations with subsequent observations on Kaua'i birds made by the authors individually and with relevant unpublished observations of other naturalists that they have generously shared with us.

We also discuss the implications of our observations for ongoing systematic controversies, including some previously unpublished supporting details for Pratt's (1979) revision of the Hawaiian honeycreepers, the basis for the classification in widest use today (American Ornithologists' Union 1983, Sibley and Monroe 1990, Tarr and Fleischer 1995). We have made some refinements of Pratt's (1979) classification, which was "eclectic" (*sensu* Raikow 1985) but based on a cladistic analysis, to make it better reflect phylogeny.

Only a few major scientific studies of Kaua'i forest birds followed our expedition: the 1981 survey made as the final part of the landmark U.S. Fish and Wildlife Service population study (Scott et al. 1986), various studies by the U.S. Forest Service (C. J. Ralph and colleagues, unpubl. data), and several surveys by other state and federal wildlife agencies (e.g., Engilis and Pratt 1989; Pyle 1990, 1994; Telfer 1993). Several species declined noticeably between 1975 and 1981, and Hurricanes Iwa in 1982 and Iniki in 1992 severely reduced remaining bird populations in the Alaka'i (Engilis and Pratt 1989; Pratt 1994a; Pyle 1983, 1993b) apparently because the montane forest birds' historic habit of riding out severe storms in lowland valleys is now maladaptive, the valleys being infested with disease-carrying mosquitoes (Atkinson et al. 1993, Pyle 1993a, Pratt 1994a). Today, the endemic Kaua'i 'O'o and Kama'o (see species accounts) may both be extinct, and the 'O'u has not been certainly reported since Hurricane Iniki in 1992 despite diligent searches by competent biologists. Among other island endemics, the Kaua'i Nukupu'u barely survives (J. Jeffrey, pers. comm.), the Puaiohi is very rare (Pyle 1994; T. Snetsinger, pers. comm.), and the 'Akikiki is proposed for listing as an

Endangered Species (T. Pratt, pers. comm.). In view of these unexpectedly rapid changes, and because the Biological Resources Division, U.S. Geological Survey, has initiated a new research program to study Kaua'i's endangered birds as the century draws to a close (T. Snetsinger, pers. comm.), a report of our 1975 work is timely.

STUDY AREA AND METHODS

Our primary study site was within what is now the Alaka'i Wilderness Preserve. We were airlifted by helicopter to headwaters of the Halehaha Stream, near one of the late John L. Sincock's (Harrison et al. 1992) study areas we call "Sincock's Bog" (Fig. 1), late in the afternoon of 1 July 1975. Our flight was hampered by low-hanging clouds and fog, but the next morning dawned bright and clear, and such uncharacteristically dry weather prevailed for the rest of our stay until just before our departure on 8 July, when clouds and fog again closed in. Each night produced heavy dew.

RJS used a Nagra portable tape recorder and a Dan Gibson parabola; HDP used a Sony cassette recorder and an 46 cm Sony PBR-400 parabola. All recordings were later archived at the Library of Natural Sounds (LNS), Cornell Laboratory of Ornithology, and some have been published (Hardy and Parker 1985; Pratt 1996). SC used binoculars and a stopwatch to record activity patterns and behaviors of several species. All 3 authors took numerous color photographs of birds, plants, and the habitat as 35 mm transparencies. A small series of specimens collected by HDP was deposited in the Museum of Natural Science, Louisiana State University.

The misnamed Alaka'i Swamp is actually a wet montane plateau mostly above 1000 m elevation spreading northwest from Mt. Wai'ale'ale, often considered the world's wettest spot, with mean annual rainfall of 1415 cm or 449 in. (Giambelluca et al. 1986). The plateau is deeply dissected by numerous forested ravines or canyons that feed into highly eroded Waimea Canyon, which drains to the south. The ridges between the streams can be broad and nearly flat, pocked in many places by open bogs (probably the origin of the "swamp" designation).

Our study area included a small (approximately 4 ha), open bog where the helicopter landed (Fig. 1). The surrounding dense rainforest was dominated throughout by 'ohi'a-lehua (*Metrosideros collina*). 'Ohi'a characteristically forms a dense canopy with numerous emergent snags (Fig. 2) that provide display perches for several native birds. The bright red brush-like 'ohi'a flowers, which lack petals, are the primary nectar source for several honeycreepers. The nectar collects in a cuplike calyx at the base of the red stamens so that nectarivorous birds must insert the bill deep into the inflorescence. The forest in the study area was very dense even at ground level and heavily overgrown with epiphytes. The epiphytic community in-



FIG. 1. Sincock's Bog as viewed from the air (upper) and from ground level (lower) with HDP in the foreground. Photos by RJS.



FIG. 2. Profile of forest canopy in the study area showing emergent 'ohi'a snags. Photo by HDP.

cludes abundant mosses and ferns as well as flowering plants.

Below the bog to the south the terrain sloped sharply to a rushing stream. In places, the banks were so steep that large 'ohi'a trees leaned over the stream almost horizontally. In other places, the streambed widened into relatively flat amphitheater-like areas that supported the growth of grass as well as small trees and shrubs. Such areas had obviously been scoured by debris during times of high water. With the help of Dr. C. H. Lamoureux, who worked from our photographs, we were able to identify many, but not all, of the dominant or common plants in the study area (Table 1).

For comparative purposes, we made a short visit to Koke'e State Park, an area just west of the Alaka'i swamp, immediately prior to our expedition. The park area differs from the heart of the Alaka'i in having much more koa (*Acacia koa*) among the canopy trees and in the presence of numerous alien plants and birds. The Koke'e region is served by many roads and trails and we have returned to it individually many times in the ensuing decades to monitor changes in Kaua'i's avian community. We mostly visited areas served by the Pihea Trail, Camp 10 (Mohihi) Road, and the Alakai Swamp Trail to the edge of the Alakai Wilderness Preserve (for maps and details see Pratt 1993).

THE AVIAN COMMUNITY

Through the 1960s, Kaua'i was considered unique among the Hawaiian Islands in having

lost none of its historically known bird species (Richardson and Bowles 1964) and the Alaka'i Plateau remained a seldom-visited wilderness. Birds in general were abundant in our study area, and native species far outnumbered aliens. Most native birds appeared to have just finished breeding. We saw few fledglings, but recently fledged immatures of several species were numerous. Except for the Kaua'i 'O'o, the Kama'o, and possibly the 'O'u, the passerines we observed did not appear to be defending breeding territories. Rather they ranged widely through the area; the species noted near our campsite changed on a daily basis. Also, few species were singing territorial songs; we recorded mostly call notes. Probably the best season for observing breeding activities in the Alaka'i would be April through June, although the peak of nesting may vary from year to year.

SPECIES ACCOUNTS

The following codes are used in this section: RE = resident, endemic Hawaiian species; RK = resident, species endemic to Kaua'i Island; RI = resident indigenous

TABLE 1. Major plant species identified in the study area, listed alphabetically within different forest strata. (Plant names follow Wagner et al. 1990).

Scientific name	Hawaiian name	Flowers	Fruit
Trees			
<i>Cheirodendron</i> sp.	'olapa		+
<i>Metrosideros collina</i>	'ohi'a-lehua	+	
<i>Myrsine</i> sp.	kolea	+	+
<i>Pelea</i> sp.	'alani	+	
<i>Tetraplasandra</i> sp.	'ohe	+	
Shrubs			
<i>Broussaisia arguta</i>	kanawao	+	+
<i>Cibotium</i> sp.	hapu'u	no notes	
<i>Clermontia</i> spp.	'oha		+
<i>Dubautia paleata</i>	na'ena'e puakea	+	
<i>Rubus hawaiiensis</i>	'akala		+
<i>Scaevola glabra</i>	'ohe naupaka	+	
<i>Vaccinium calycinum</i>	'ohelo kau la'au		+
<i>Vaccinium dentatum</i>	'ohelo	no notes	
Herbs and Epiphytes			
<i>Adenophorus</i> sp.	unknown	no notes	
<i>Astelia</i> sp.	pa'iniu	+	
<i>Carex</i> sp.	unknown	no notes	
<i>Dianella sandwichensis</i>	'uki 'uki	+	+
<i>Drosera anglica</i>	mikinalo	+	
<i>Freycinetia arborea</i>	'ie'ie	no notes	
<i>Korthacella remyana</i> var. <i>wawrae</i>	hulumoa	+	+
<i>Lycopodium cernum</i>	wawae 'iole	+	
<i>Lycopodium serratum</i>	unknown	+	
<i>Nertera granadensis</i>	unknown		+
<i>Psilotum</i> sp.	moa	no notes	
<i>Smilax sandwichensis</i>	hoi kuahiwi	+	
<i>Viola kauaensis</i>	poke hiwa	+	+

breeding species; A = alien breeding species. Federally recognized Endangered Species are noted as such.

White-tailed Tropicbird or Koa'e-kea (*Phaethon lepturus dorotheae*), *RI*.—We saw two individuals flying over bog at about 13:00 8 July, as we awaited our helicopter pickup. Tropicbirds are numerous in canyons and valleys throughout Kaua'i and nest in Hanapepe Valley south of our study area (HDP pers. obs.).

Hawaiian Duck or Koloa (*Anas wyvilliana*), *RE*, *endangered*.—RJS flushed one individual from the stream bed just below camp. The bird was in a wide part (about 15 m) of the stream where it was probably standing on a rock or in a dense growth of sedge (*Carex* sp.). The duck is also present in low numbers and may nest along Kawaikoi Stream in the Koke'e area. Although Hawaiian Ducks con-

centrate in lowland wetlands such as the taro fields at Hanalei (Pratt 1993), they also nest in the mountains (Berger 1981).

Red Junglefowl or Moa (*Gallus gallus*), *A*.—HDP flushed one bird from the ground in the low forest north of the bog on 4 July, and found an abandoned large nest on the ground in the same area. We did not hear any dawn "crows" from our campsite. The unusually large numbers of these birds that congregate around buildings in Koke'e State Park are apparently lured there and maintained by food handouts from visitors.

Short-eared Owl or Pueo (*Asio flammeus*), *RI*.—Solitary individuals were observed soaring, possibly hunting, a few meters above the tree tops once or twice each day, usually in the afternoon or early evening. The owl is also uncommon in the Koke'e region. Although historically regarded as an endemic subspe-



FIG. 3. Juvenile Kaua'i 'Elepaio. Photo by HDP.

cies, this cosmopolitan species may be a post-Polynesian colonizer of the Hawaiian Islands (Olson and James 1991).

Kaua'i 'Elepaio (*Chasiempis sclateri*), *RI*.—In 1975, only one species of 'elepaio was recognized, with subspecies on Kaua'i (*C. sandwichensis sclateri*), O'ahu (*C. s. gayi*, later emended to *C. s. ibidis* by Olson 1989a), and Hawai'i (*C. s. sandwichensis*). Subsequently, the Hawai'i form was shown to exhibit intra-island variation at the subspecies level, with at least three forms recognizable (Pratt 1980). The striking plumage differences of the Kaua'i and O'ahu forms clearly qualify them as "megasubspecies" (sensu Amadon and Short 1976), and they are unquestionably "phylogenetic" species (sensu Cracraft 1983). Olson and James (1991; see footnote to Table 1) recognized three species of *Chasiempis*, but whether they consider them biological or phylogenetic species is unclear.

Our work on Kaua'i combined with observations on other islands (Conant 1977, Pratt 1980) supports the recognition of three biological species of *Chasiempis*. The adult Kaua'i 'Elepaio is the plainest and the only one with a gray dorsum. Juveniles are mostly rufous, without the white rump and wing-bars of the adults, and closely resemble juveniles of the O'ahu form in color but seem subjectively to be subtly different (more rotund, less linear) in shape (Fig. 3). Plumage dimorphism is lacking in adults on Kaua'i and O'ahu, but Hawai'i adults are strongly dichromatic (Pratt 1980, Pratt et al. 1987).

The variations in tempo and pitch of the vocalizations of the Kaua'i 'Elepaio have not

been thoroughly investigated, but the repertoire is qualitatively distinguishable from those of the O'ahu and Hawai'i forms (Pratt 1996). E. VanderWerf (pers. comm.) recently found that O'ahu 'Elepaio respond differentially to playback of their own vocalizations and those of Hawai'i birds. Similar studies with the Kaua'i 'Elepaio are ongoing. All 'elepaio are bold and inquisitive, but the Kaua'i birds are particularly so, the juveniles more than adults. Juvenile Kaua'i 'Elepaio approach humans closer, sometimes perching within arm's reach, and follow them farther than do 'elepaio on other islands. Both age categories respond readily to imitations of their whistled songs and calls as well as "spishing." We saw several fledglings including one whose rectrices were only 1–2 cm long. This suggests that the breeding season ends about the same time as that of the O'ahu 'Elepaio (Conant 1977, Sherwood 1995), but earlier than that of the Hawai'i representative (Bollinger and Bollinger 1987).

Ecologically, all three 'elepaio species are forest birds, but as their islands differ, so do the birds' respective habitat preferences. We observed both adult and immature Kaua'i 'Elepaio frequently every day in our study area, and found them also common at Koke'e. They are restricted to the higher and wetter parts of the island (Scott et al. 1986) and have not undergone any obvious decline since 1975 (Engilis and Pratt 1989, Walther 1995). In contrast, the O'ahu 'Elepaio has declined strikingly during the same period (Williams 1987, Pratt 1994a, Conant 1995) and is now rare, with a fragmented distribution restricted primarily to relatively mesic valleys at middle elevations (VanderWerf et al. 1997). It has apparently always been more common in drier, mid-elevation forests (Bryan 1905). On Hawai'i, the intra-island variation in plumage color is correlated with rainfall (Pratt 1980).

Apparently the three *Chasiempis* were first "lumped" by Bryan and Greenway (1944), who gave no data to support the change in status; and subsequent authors, until Olson and James (1991), accepted that taxonomy by default. We believe a return to recognition of three species, with *C. sandwichensis* having three intra-island subspecies, provides a more meaningful and balanced taxonomic treatment that better reflects the observed geographic

variation. Because the three forms are allopatric, biological species limits must be assessed by inference. Our observations, as well as those of VanderWerf (in press), show that the striking plumage differences are backed up by potential behavioral and ecological isolating mechanisms. We can discern no reason, other than the general similarities reflected at the generic level, to consider them conspecific.

Kama'o (*Myadestes myadestinus*), *RK*, *endangered*, *possibly extinct*.—This larger of the two Kaua'i solitaires (Pratt 1982), then called the Large Kaua'i Thrush, was not uncommon in the study area during our visit. As many as seven individuals could be seen simultaneously perched on emergent 'ohi'a snags in the forest surrounding the bog above our camp in the early morning and at dusk. They perched upright with the tail down. From inside the forest, Kama'o were difficult to see, but we heard their songs and calls throughout the day in the vicinity of the campsite. They gave two different calls, one a cat-like rasp and the other resembling the sound of a police whistle. These calls are similar to, but distinguishable from, calls of the 'Oma'o (*M. obscurus*) of Hawai'i. The song of the Kama'o is entirely different from that of the Hawai'i bird and resembles closely the song of Townsend's Solitaire (*Myadestes townsendi*) of western North America, with some of the tonal quality of the song of the Slate-colored Solitaire (*M. occidentalis*) of Mexico. These song differences were among early indications that the Kama'o and 'Oma'o were separate species, later confirmed by Pratt's (1982) playback experiments on Hawai'i using recordings made during our Alaka'i visit. The song of the Kama'o is long and complex with an ethereal, echoing, and cascading quality. A typical singing performance ended with the bird rising on its wings, hovering over the forest while singing constantly, and then abruptly diving into the trees. Pratt (1982) presented sonagrams of the two call types and the song, and recordings of all three have now been published (Pratt 1996). What was once Kaua'i's most abundant forest bird (Munro 1944) may well be extinct; it has not been seen since Hurricane Iniki (Walther 1995; T. Snetsinger, pers. comm.). A February 1989 survey by the Hawaii Division of Forestry and Wildlife (DFW) reported two "prob-

able" sightings, but no birds were heard (Pyle 1989). That report noted that on a 1985 DFW survey many Kama'o were heard. DFW again surveyed the Alaka'i Swamp in 1993, and two "brief but inadequate" possible sightings of Kama'o were reported (Pyle 1993b).

Puaiohi (*Myadestes palmeri*), *RK*, *endangered*.—Our first sighting of this species occurred at dusk on 3 July. A single bird flew from the forest underbrush and perched silently above our camp site. In the fading light we could see the bird was a heavily spotted immature, with a few down feathers still clinging to the head. The pink feet were evident as the bird perched upright facing us. Later, HDP saw two other individuals, both adults. One was located by slowly searching out the source of a dry, toneless hiss that proved to be the call note. The bird was perched almost motionless on a mossy stump under a concealing clump of vines and shrubs at the upper rim of a small ravine. In posture, this individual resembled the bird seen previously, as it sat bolt upright rather in the manner of a tyrannid flycatcher. It remained for some minutes in this position, uttering its calls at about 10-s intervals. It then flew to the end of a small stump that extended from a high bank over the stream. Again, the bird remained motionless for some minutes and then flew away into the forest. The third individual was glimpsed briefly as it flushed from concealment in a small (ca. 5 m) 'olapa (*Cheirodendron trigynum*) tree that grew in a wide, flat area of the streambed (Fig. 4). These observations demonstrate that this species is extremely difficult to detect where it occurs, and thus may have been more common in the Alaka'i than the few published observations would indicate. All of our sightings were in or near a deep, protected stream valley, as have been other observations (Ashman et al. 1984, Kepler and Kepler 1983, Pyle 1984), whereas most of the Kama'o we observed were near the more exposed ridge-top bog. The smaller solitaire appears to be a ravine specialist. This may partly explain why the Puaiohi, although historically much the rarer of the two Kaua'i thrushes (Perkins 1903), has weathered the two recent hurricanes much better than its larger relative. A very small population of Puaiohi persists in the Alaka'i (T. Snetsinger, unpubl. data) and is the subject



FIG. 4. An open area of stream bed on Halehaha Stream where HDP flushed a Puaiohi. Photo by HDP.

of intense observation and possible recovery actions by federal agencies and The Peregrine Fund. These ongoing studies have already discovered a larger than expected population (Pyle 1996) in the Koai'e Stream area (almost directly between Koke'e and our 1975 study site) where two nests were found about a decade ago (Ashman et al. 1984, Kepler and Kepler 1983).

Melodious Laughing-thrush (*Garrulax canorus*), A.—RJS briefly saw one bird in low, dense vegetation above the campsite. On Kaua'i, this bird is found in dense mesic and wet forests of both native and introduced plants. It is very secretive and almost always seen near the ground. Its loud song is the best indication of its presence. Although we have no record of vocalizations in our field notes, HDP later noticed the song in the background of one of his tapes.

Japanese White-eye (*Zosterops japonicus*), A.—White-eyes were present in the area but were greatly outnumbered by native birds. We saw only a few small groups. In contrast, they were common to abundant in the Koke'e area.

This introduced species has become the most abundant forest bird on Kaua'i (HDP, pers. obs.; Scott et al. 1986).

Kaua'i 'O'o or *'O'o'a'a* (*Moho braccatus*), RK, *endangered, possibly extinct*.—On 2 July we awoke to the song of the 'o'o (06:15). Shortly after the dawn chorus ceased and the sun was up, a single 'o'o appeared near our campsite and provided our first look. Interestingly, the bird did not visit us on subsequent mornings, indicating that it may have deviated from its usual feeding route to "check us out" that first day. The song (for recordings see Pratt 1996) is a series of loud, clear melodious whistles with a "tune" reminiscent of the song of the Western Meadowlark (*Sturnella neglecta*). Its tone quality is distinctly meliphagine, however, with a haunting, echoing quality, and is surprisingly similar to portions of the song of the Tui (*Prosthemadera novae-seelandiae*) of New Zealand (for an example of the latter, see Gunn and Gullledge 1977). Other portions of the Tui song sound remarkably like the unrelated drepanidine 'I'iwi (discussed below). The Kaua'i 'O'o's song is

TABLE 2. Percentage of time devoted to 7 activities of 2 Kaua'i 'O'o during 61 minutes and 36 seconds of observation.

Activity	Percentage of time
Feeding at flowers	55
Inactive perching	29
Preening	9
Flying or hopping	3
Singing	3
Insect gleaning ^a	<1
Territorial chasing ^b	<1

^a We feel this value is somewhat low based on many other untimed hours of observation.

^b The pair was defending an apparent feeding territory, primarily against 'I'iwi and 'Apapane.

much more complex than those of the other species of *Moho* (Perkins 1903), but includes two-note phrases that probably resemble the "oh-oh" for which the birds were named. Each day birds sang at 10–20 min intervals until about 10:30, when song became less frequent. Duetting by the pair was frequent throughout the day. A sharp two-note whistle, which can be heard in the second cut of this species presented by Pratt (1996), appeared to be an alarm or alert call-note.

On 3 July we located an apparent feeding territory of a pair of Kaua'i 'O'o downstream from our camp. It included several large, heavily flowering 'ohi'a trees from which the pair excluded all other birds, a size-based hierarchy similar to that reported on Maui (Carrothers 1986) and Hawai'i (Carpenter and MacMillen 1976). We surmised that the birds had several such feeding areas or territories

that they patrolled systematically because they would leave this area for 20–40 min at a time, usually flying off to the northeast and returning northwest. This foraging pattern is consistent with observations of "trap-line" feeding in East Maui. There, both the 'I'iwi and the 'Akohekohe (*Palmeria dolei*) revisit blooming 'ohi'a trees with a regular cyclicality of about 20–35 min (HDP pers. obs.). Probably the cycle is set by the rate of nectar production of *Metrosideros*. Besides taking nectar from 'ohi'a flowers the birds foraged for insects from masses on the larger branches and among small branches and foliage. One bird ate small black 'olapa berries. Hart (1978) also reported a bird eating 'olapa fruits, and saw a bird taking insects from moss clumps. The birds moved quickly and decisively through the trees often holding the tail cocked in a nearly vertical position (Frontispiece). SC timed various behaviors of two birds with a stopwatch, and used data to characterize activity patterns and foraging behavior (Tables 2 and 3).

We were able to confirm the presence of only one pair of Kaua'i 'O'o, although on one occasion we may have heard a third individual call in the distance while both birds were under observation. By 1981, only a single known pair survived, possibly the same birds we observed (Scott et al. 1986). The female of the last known pair was not found after Hurricane Iwa (Pyle 1983), and the male was last seen in 1985 (Pyle 1989). The last report of this species was that of Cynthia and James

TABLE 3. Foraging behavior of two Kaua'i 'O' during 47 minutes and 11 seconds of observation (data recorded only while birds were feeding).

Vertical canopy occupation		Horizontal canopy occupation	
Height (m)	Percent time	Zone ^a	Percent time
2–4	18	Inner	14
4–7	11	Center	<1
>7	71	Outer	86
Movement Patterns During Feeding			
Percent time moving		57	
Percent time stopped (feeding pause)		43	
Rate of feeding pauses		3.9 pauses/min	
Rate of movement (not including feeding pauses)		2.1 m/min	
Rate of movement (including feeding pauses)		1.2 m/min	
Average distance between feeding pauses		0.3 m	

^a Canopy zones: Inner = within 1 m of the central axis of tree; Outer = within 1 m of outermost crown foliage; Center = between inner and outer.



FIG. 5. 'O'u (*Psittirostra psittacea*) male (l.) and female (r.). Photos by RJS. See also Frontispiece.

Krakowski, who heard an 'o'o calling on 28 and 29 April 1987 (Pyle 1987). A survey by state agency biologists in February of 1989 found no 'o'o, and the report speculated that the birds were "now probably gone" (Pyle 1989). They have not been reported since and are undoubtedly extinct, their loud vocalizations being difficult to overlook.

Northern Cardinal (*Cardinalis cardinalis*), A.—SC heard one bird singing the morning of 8 July for our only observation. Northern Cardinals were and remain common to abundant at Koke'e, where the forest is more disturbed. In general, they are one of the more widespread introduced birds throughout the Hawaiian Islands, but are rare in primary forest (Pratt et al. 1987).

'O'u (*Psittirostra psittacea*), RE, possibly extirpated.—We located several pairs of 'O'u near our campsite (we estimated about one pair per 4 ha). They were usually heard before they were seen, giving their characteristic, loud, mellow, upslurred call-note, but were difficult to locate because the call is ventriloquial. SC saw males singing on several occasions, but was unable to record the song, a complex canary-like performance, starting with two downwardly inflected notes, followed by a short, upslurred note, and a descending warbling trill and ending with a low downwardly inflected note of about the same frequency as the second note. HDP also noted a single short song, comprising whistles and a trill, that he was unable to record but transliterated as *fee-too-ter-wheet-wheet-wheet-wheet-wheet-fee-too*. When the males sang, they fluffed all the body plumage and flapped

their wings clumsily. The bill was open during singing and the body quivered slightly.

All the birds we saw sat quietly or moved slowly and heavily in upper portions of dead snags or on high exposed perches. As a result, most of our photographs, which appear to be the only ones ever taken of this species, are strongly back-lighted and fail to show the birds' colors to good effect. Their perching posture was distinctively horizontal, with the tail held slightly up but not cocked. They appeared rather pot-bellied (Fig. 5, Frontispiece). Although we spent several hours watching various individuals, HDP saw only one bird actually feed, apparently taking nectar from an 'ohi'a flower.

A Kaua'i 'O'u population in the low hundreds in the late 1970s was apparently decimated by Hurricane Iwa in 1982 (Pyle 1983, Engilis and Pratt 1989). The last published Kaua'i sightings were made on 16 and 17 February 1989 (Pyle 1989). The population on Hawai'i has likewise dwindled, and there have been no recent reports of 'O'u on that island. The 'O'u is on the brink of extinction, if any yet survive.

Kaua'i 'Amakihi (*Hemignathus kauaiensis*), RK.—This was the scarcest of the "common" honeycreepers in our study area, and was observed on only three occasions. HDP saw an individual near the camp on 6 July, and above it on 8 July. The first bird was clinging to a vertical 'ohi'a trunk and picking over the bark, very much the way the 'Akikiki forages. SC and RJS observed a bird feeding on 'ohe naupaka (*Scaevola glabra*) flowers, which are 4–6 cm long. To obtain nectar, the bird in-

serted its head into the bright yellow tubular corolla, rather than piercing a hole at the flower base as we have seen other Kaua'i 'Amakihi do at morphologically similar flowers. It also took insects from around flower bases.

At Koke'e, with more koa, the Kaua'i 'Amakihi was common in 1975 and remains so today (HDP, pers. obs.). We attribute its rarity in the study area to the absence of koa. In 1975, the Kaua'i 'Amakihi was regarded as one of four subspecies of 'Amakihi (*H. virens*), although Bock (1970) considered its bill size differences sufficient to separate it specifically from other 'amakihis. The bill is much larger than those of other 'amakihis, with little or no overlap in measurements (Fig. 6). Interestingly, the recently split O'ahu 'Amakihi (*H. chloris*), the Kaua'i bird's apparent closest relative (Tarr and Fleischer 1994), shows the least approach or overlap of all. Birders inexperienced on Kaua'i may fail to appreciate the degree of difference and consequently misidentify a Kaua'i 'Amakihi as a Nukupu'u (discussed below). Therefore, reports of Nukupu'u on Kaua'i should be regarded with some skepticism unless accompanied by unequivocal details.

Our 1975 observations and subsequent studies (Pratt 1979) found potential isolating mechanisms of the Kaua'i 'Amakihi among ecological and behavioral characters. The bird spends much more time picking prey from the bark of trees and less time feeding among leaves and flowers than other 'amakihis. Rai-kow (1974) found such distinctive foraging behavior to be innate. The typical call of both the Common 'Amakihi and the O'ahu 'Amakihi is a short, buzzy or mewing note rather similar to the call of the Blue-gray Gnatcatcher (*Polioptila caerulea*) of eastern North America. The Kaua'i 'Amakihi also utters such a note, but only occasionally. Its typical call is a loud upslurred chirp (Pratt 1996), sometimes indistinguishable from calls of 'Anianiau, 'Akeke'e, and 'Akikiki, all of which join mixed flocks on Kauai. All 'amakihis sing short trills (Pratt et al. 1987, Pratt 1996), but the loudest notes of the Kaua'i bird's trill usually drop in pitch whereas those of the other forms remain level. The repeated elements of the Kaua'i bird's trill appear simpler in sonagrams, and the song also usually has a distinctive introductory note that is not

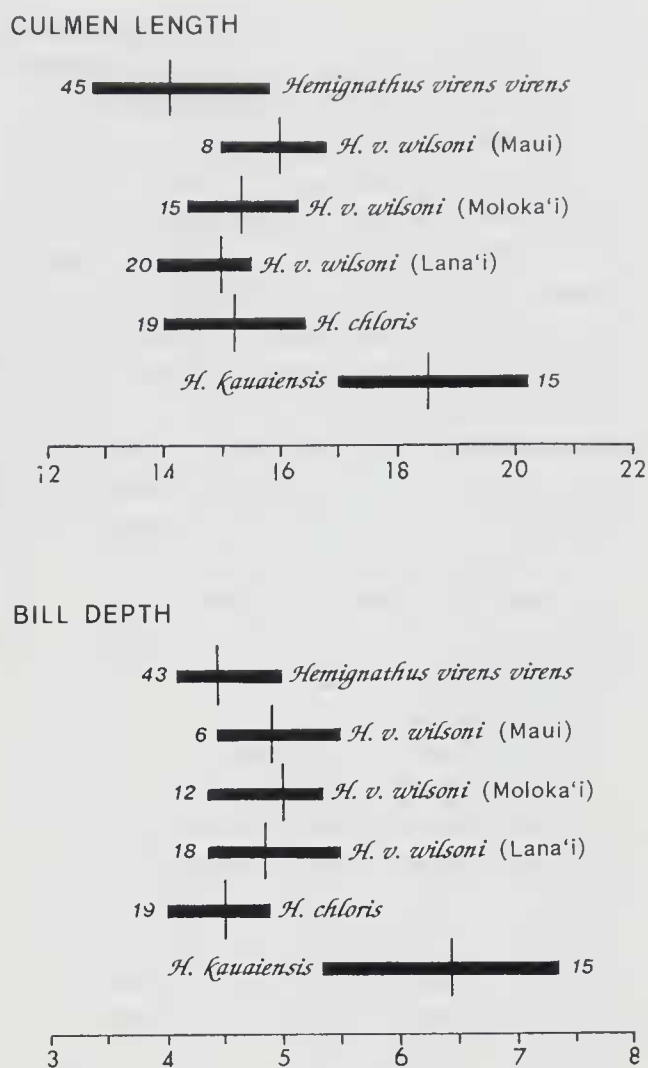


FIG. 6. Bill measurements of 'amakihis from various islands, adapted from Pratt (1979). Means are indicated by long vertical lines, ranges by horizontal bars. All measurements in millimeters. Number of specimens examined at ends of bars.

present in 'amakihi songs from other islands (Pratt 1996). Individual trills of *H. virens* typically last about two seconds, but those of *H. kauaiensis* are about a half-second shorter. Further, although the songs of all species are variable, the Kaua'i bird seems to have a wider range of variation that includes trills on a nearly level pitch. This observation may explain why birds on Hawai'i that responded to songs of conspecifics from Maui failed to respond to playback of Kaua'i songs, whereas Kaua'i birds responded equally to either tape (Pratt 1979). Kaua'i birds may have recognized the level-pitched trills as within their range of variation, but Hawai'i birds did not recognize the descending trills from Kaua'i.

Based on the large suite of potential isolating mechanisms and a level of morphological

differentiation comparable to species-level rank in other passerines, Pratt (1979) and Pratt et al. (1987) recognized the Kaua'i 'Amakihi as a species, as did James and Olson (1991), on the basis of osteological studies and Johnson et al. (1989) and Tarr and Fleischer (1994) based on biochemical studies. The American Ornithologists' Union (1995) has now recognized the split. The Kaua'i 'Amakihi's taxonomy is rather convoluted because its generic placement has been controversial. The correct specific epithet depends on whether one places the 'amakihis in *Hemignathus* or in some other genus. The specific epithet of the Kaua'i 'Amakihi is *stegnegeri* in any genus other than *Hemignathus*, where that name is preoccupied (Olson and James 1988). Pratt (1989a) proposed *kauaiensis* as a replacement in *Hemignathus*.

Historically, *Hemignathus* was used either for the 'akialoas, with the bill greatly elongated, and the nukupu'us, with a short mandible and elongated maxilla, together (Amadon 1950), or for the 'akialoas alone with the nukupu'us segregated as *Heterorhynchus* (e.g., Perkins 1903). Olson and James (1995) pointed out that both names are based on the same type species; they restricted *Hemignathus* to the nukupu'us and named the genus *Akialoa* based on the Hawaiian name for those birds. Pratt (1979) was the first to place the similarly plumaged but short-billed 'amakihis in *Hemignathus*, although R. C. L. Perkins (*in* Wilson and Evans 1890–99) also considered the 'amakihis closer to the 'akialoas and nukupu'us than to the 'akepas (*Loxops*) with which Amadon (1950) grouped them. Olson and James (1995) denigrated those (e.g., American Ornithologists' Union 1983, Sibley and Monroe 1990, Tarr and Fleischer 1995) who followed Pratt's (1979) classification, stating wrongly that it was adopted "without any consideration having been given to its merits" (Olson and James 1995:374). Because the observations we began in 1975 in the 'Alaka'i Swamp were seminal in the development of Pratt's (1979) taxonomy, we herewith reconsider its merits, as compared to the classification of the Olson/James team (see also Pratt 1994b).

Pratt's (1979) classification was based on the literature dealing with tongue morphology, breeding biology, myology, and osteology as

well as firsthand investigations of plumage coloration and ontogeny, sexual dimorphism, vocalizations, foraging behavior, and ecology. Qualitative characters such as bill shape and plumage pattern were the most useful in delimiting genera, whereas such characters as tongue morphology and, surprisingly, vocalizations proved more useful as indicators of higher relationships. Numerous recent studies have shown that the traditional prejudice against the use of plumage color in alpha taxonomy (as stated by Amadon 1950:166 and clearly evident in many other works of that era) has no justification. In the two other most frequently cited avian examples of adaptive radiation, the Vangidae (Langrand 1990) and Geospizinae (Lack 1968, Grant 1986), plumage pattern is as good a predictor of relationships as any external character, and is much more useful in delimiting genera than bill size or length, a character that Amadon (1950) apparently considered pre-eminent and reiterated in his critique of Pratt's (1979) revision (Amadon 1986). Members of Pratt's *Hemignathus* have sharply pointed downcurved bills that are dark colored with a pale base to the mandible. Adults are dull green above and more or less yellow below, with narrow dark lores. Sexual dimorphism is pronounced, with males larger, longer billed, and always yellower than females. Juveniles resemble adult females but have pale wing-bars (retained in adult females of *H. chloris*). The bill shape and most of the suite of color characters differ from the ancestral condition in Drepanidinae (Raikow 1977), are not found among the Carduelinae (for illustrations of all species see Clements 1993), and can only be regarded as synapomorphies. Except for the 'Anianiau (discussed below), which we no longer consider to belong to the genus, the various *Hemignathus* are so similar in plumage at any age and in either sex that the bill would have to be seen to confirm identification in the field (Pratt et al. 1987). Some other avian genera (*Calidris*, *Nectarinia*, *Toxostoma*, and *Geospiza* come to mind) exhibit a similar range of variation in bill length and shape.

James and Olson (1991) based their alternative classification primarily on cranial osteology, particularly the feeding apparatus, because the postcranial anatomy of Hawaiian honeycreepers is so uniform as to provide lit-

tle phylogenetic information (Raikow 1977). Because they were classifying numerous recently found subfossils, their focus on osteological characters was understandable, and they stated forthrightly (James and Olson 1991:23) that they had not attempted a phylogenetic analysis. In their most recent revision, Olson and James (1995) recognized the genera *Akialoa* and *Hemignathus* (nukupu'us only) with the 'amakihis being placed in *Loxops* along with the 'akepas and the Hawai'i Creeper ("L." *mana*). In so doing they reconstituted Amadon's (1950) *Loxops*, minus the three species of *Paroreomyza* and the 'Akikiki (discussed below).

Amadon's (1950) *Loxops* is probably the most extreme example of alpha-level taxonomic over-lumping in the annals of avian systematics. It included one species of cross-billed 'akepa, now shown to be at least two biological species (Pratt 1989b); four subspecies of curve-billed 'amakihi now regarded as three species (Tarr and Fleischer 1994); the nearly straight-billed Greater 'Amakihi (*Viridonia sensu stricto*) which may be related to the newly discovered fossil genus *Aidemedina* (James and Olson 1991); the 'Anianiau (*Magnumma*, discussed below) which may not be closely related to the 'amakihis after all (Tarr and Fleischer 1995); and a "species" Amadon called "the Creeper" now regarded by all authors as five species in two (Pratt 1992b) or three (Olson and James 1982, James and Olson 1991) possibly unrelated genera! The only conceivable character these birds have in common is a short bill (Pratt 1979). The removal of four of Amadon's "subspecies" of "creeper" from his *Loxops* does not make the genus any more tenable. It has no defining synapomorphies or even any general similarities to unite its disparate members. Olson and James (1995:375) stated misleadingly that unpublished genetic studies by R. Fleischer support their treatment "...with the proviso that the 'akialoas have not yet been analyzed and that the amakihis may need to be further split." They fail to mention that Tarr and Fleischer's (1995) recently published findings lend equal support to Pratt's treatment, depending on which of two algorithms one follows, and even then the genetic studies say nothing about where generic limits should be set among closely related groups. Obviously,

biochemical studies do not always resolve systematic disputes.

A classification compatible with both views would recognize the genus *Viridonia* for the 'amakihis with *Loxops*, *Akialoa*, and *Hemignathus* as separate genera. We consider this a counsel of despair, however, because it would turn back the taxonomic clock a century, when nearly every species of Hawaiian honeycreeper had its own genus. Such a classification is devoid of phylogenetic information and ignores demonstrated synapomorphies that cluster the three curve-billed green drepanidine groups. The only way to taxonomically recognize that cluster is to consider it a genus with *Viridonia*, *Hemignathus*, and *Akialoa* (but not *Loxops*) as subgenera because the entire drepanidine taxon, once considered a family, may be only a tribe (Sibley and Monroe 1990; James and Olson 1991).

'*Anianiau* (*Magnumma parva*), *RK*.—This bird was common, and we observed it frequently every day taking nectar and probably insects from 'ohi'a flowers. Birds foraged in the tops of flowering trees along with 'Akeke'e and 'Apapane, but we saw no interspecific aggression. Occasionally the 'Anianiau foraged much lower, particularly among kanawao (*Broussaisia arguta*) plants. On 8 July SC observed a single individual taking nectar by inserting its bill into the tubular corollas of 'ohe naupaka (*Scaevola glabra*) flowers. When 'ohi'a is not in full bloom, the 'Anianiau is an active and agile insectivore, seeking its prey among smaller branches and leaves (Raikow 1974, HDP pers. obs.). In its movements and postures it resembles a wood-warbler (*Parulinae*).

HDP saw an adult feeding a fledgling barely able to fly on 8 July. July may be the last month of the breeding season. Hart (1976) saw a male giving courtship displays before a female on 26 May 1976. Berger et al (1969) suggested that the nesting season of this species extends from mid-February to late June. We heard no singing by this species in our study area, but had learned the song, a trill of doublets or triplets, during our prior visit to Koke'e. The typical call note is a 2-syllable *tew-weet*, the first note low, the second rising. Other calls resemble those of Kaua'i 'Amakihi, 'Akeke'e, and 'Akikiki. The 'Anianiau remains as common today as it was in 1975,

despite an apparently temporary reduction in numbers following Hurricane Iniki (HDP, pers. obs.). It is by far the most abundant of the "green" honeycreepers in the Koke'e area.

When first described, the 'Anianiau was placed in the genus *Himatione* (which, at the time, included the 'amakihis and the "creepers") but was thought to be closer to the creeper group than to the 'amakihis (Wilson and Evans 1890–99:xxi). As the species became better known it was placed with the 'amakihis in *Chlorodrepanis* (Perkins 1903), and some authors even used the English name "Lesser Amakihi" for it. In his eclectic classification, Pratt (1979) uncritically accepted the 'amakihi relationship and placed the 'Anianiau in *Hemignathus*. Although it is a yellow-green bird that resembles the 'amakihis behaviorally, close examination reveals that the 'Anianiau lacks the defining synapomorphies of *Hemignathus*. Sexual dimorphism is much less pronounced than in 'amakihis, nukupu'us, and 'akialoas, and the dark lores are totally lacking. The bill is short, only slightly downcurved, and flesh-colored with a dusky culmen. A cladistic reinterpretation of Pratt's (1979) classification would place the 'Anianiau in its own monotypic genus between *Loxops* and *Hemignathus*. The phylogeny of those three genera cannot be resolved on the basis of present knowledge. This taxonomy is consistent with Tarr and Fleischer's (1995) genetic studies (although not predicted by them), whichever algorithm one follows, as well as with those of Johnson and coworkers (1989). Mathews (1925) proposed the generic name *Magumma* as a replacement for the preoccupied *Rothschildia* so that a name would be available if the 'Anianiau was ever placed in its own genus.

Kaua'i Nukupu'u (*Hemignathus lucidus* hanapepee), RK, endangered.—A single bird, observed by SC, perched on the top of an 'olapa tree for about 30 seconds at 19:00 on 4 July. This subspecies is extremely rare, and, at the time, had been seen on only two occasions (Sincock in Haley 1975) since its rediscovery in 1960 by Richardson and Bowles (1964). The USFWS forest bird survey in 1981 failed to find any Nukupu'u, but 1985 saw a flurry of credible sightings in several localities (Pyle 1985a, b). Reports in the

Koke'e area by isolated observers (Pyle 1985b, 1988, 1992) have lacked sufficient details for unequivocal elimination of Kaua'i 'Amakihi (discussed above). The Nukupu'u differs from the 'amakihi in having the head paler (bright yellow in males, duller in females) without a contrasting darker crown and a darker, thinner-based bill (Pratt et al. 1987) and it virtually never feeds in flowers (Perkins 1903).

Because searches immediately following Hurricane Iniki failed to find any Nukupu'u (Pyle 1993c), many feared that it shared the fate of the Kama'o. However, on 10 May 1995, while conducting bird surveys along the Mohihi-Waiialae Trail near Koai'e Stream, T. L. C. Casey (pers. comm.) heard a short whistle, resembling one call of the Maui Parrotbill (*Pseudonestor xanthophrys*), that turned out to be given by a Nukupu'u. Her notes include a detailed description of the bill as "...longer and slimmer than [that of] a Kaua'i 'Amakihi, particularly at the base where the [bill of the] Kaua'i 'Amakihi is quite heavy." She identified the bird as a female on the basis of its dull yellow head and noted that it "...spent several minutes foraging through branches of 'ohi'a and 'olapa, working each branch upwards from side to side." Casey watched the bird for about three minutes as it foraged with a mixed-species flock of small birds that included 'Anianiau and Kaua'i 'Amakihi. This observation is consistent with Perkins' (1903) report that Nukupu'u often accompany such flocks.

In the same general area, Casey saw a male Nukupu'u on the morning of 22 June 1995. It gave a call similar to that of the previous bird but showed a much brighter yellow head. Later the same day at the same locality, J. Jeffrey (pers. comm.) observed a female Nukupu'u for approximately 30 seconds. His descriptions, particularly of the bird's behavior are definitive. He noted that when foraging, "the bird used its bill to rip open the thin bark and wood and probe with the upper bill [showing] that the maxilla was longer than the mandible and that the mandible was also curved downward. To feed, the bird appeared to push the maxilla into or under the bark or soft wood then pull back on the maxilla while using the mandible as a fulcrum, tearing the bark or wood." Although these sightings seem to in-

dicate the presence of at least one pair at this locality, other observers (D. Kuhn, J. Lepson, pers. comms.) subsequently failed to find any Nukupu'u there. This species' long term survival at very low numbers is quite remarkable.

Kaua'i 'Akialoa (*Hemignathus stejnegeri*), *RK, endangered, extinct*.—This was the only historically known Kaua'i forest bird that we failed to see during our 1975 expedition. Following the 1960 rediscovery of this species (Richardson and Bowles 1964), the only detailed published report of it was that of Huber (1966) of a sighting in 1964 in the same general area as those of 1960. His description of the bird's awkward use of its extremely long bill as it fed among 'ohi'a flowers is convincing. The Kaua'i 'Akialoa was both an insectivore that probed among epiphytic mosses, lichens, and ferns and a nectarivore that fed on deep lobelioid flowers as well as the more open flowers of 'ohi'a (Perkins 1903, Richardson and Bowles 1964). Although details have not been previously published, P. L. Bruner (pers. comm., Pratt et al. 1987) saw a Kaua'i 'Akialoa in 1969. An undergraduate and beginning ornithologist at the time, he was taken to a spot by local hunters and shown the bird, but could not reconstruct the exact locality. Apparently it was on land owned by Gay and Robinson, because his guides were former employees of that corporation, and thus it was not the same place as the previous sightings. In conversations with HDP in 1971, Bruner described the bird's head-down probing of the undersides of large branches and reported being surprised by the bird's very large size, an attribute that would not have been apparent to him from the popular literature of the time (e.g., Peterson 1961, which gives a deceptively small rendering). Only later, upon examining specimens, did HDP come to realize how much bigger the 'akialoa was than other green honeycreepers on Kaua'i. We are convinced that Bruner was the last person to see a Kaua'i 'Akialoa.

Huber's (1966) report contains an enigmatic description of the 'akialoa's call. He saw the bird in the same tree as an 'O'u that was characteristically sitting so motionless that he failed to notice it at first. He stated that both birds were calling and that the notes were identical except that one was upslurred, the other downslurred, and he could not remem-

ber two years later which was which! As noted earlier, we heard many 'O'u whistles that were upslurred. Thus, we were intrigued by a downslurred whistle, recorded by both RJS and HDP, we heard late in the afternoon of 2 July 1975 northwest of Sincock's Bog. The author of this call was too far away in dense forest for us to see it (the sun was setting at the time), and we never heard the downslurred call again. Did we, in fact, hear the "last" Kaua'i 'Akialoa? The question remained open until 1989, when A. Engilis (pers. comm.) heard a similar call and saw that it was uttered by an 'O'u. On that basis, and because Huber may well have heard the call of an unseen 'O'u and attributed it to his 'akialoa, Pratt (1996) presented our downslurred call as "'O'u, Call 2." Noteworthy is that Perkins (1903) described no similar note for the Kaua'i 'Akialoa but instead described its calls as distinct but intermediate between those of its congeners, the Kaua'i 'Amakihi and the Nukupu'u. Nevertheless, we will probably always be haunted by our unseen whistler.

'Akikiki (*Oreomystis bairdi*), *RK, proposed endangered*.—Although we observed 'Akikiki (formerly called Kaua'i Creeper) every day, they were not as common as 'Elepaio, 'Akeke'e or 'Apapane. The 'Akikiki forages by creeping along larger branches and takes prey from the bark surfaces, crevices, lichens, and mosses. One bird spent three minutes taking insects from the bases of 'ohi'a inflorescences (SC, pers. obs.). HDP noted several family groups consisting of immatures and a pair of adults. The young were fully feathered and seemingly adept at foraging but still begged. Immatures are distinguished by white "spectacles" (Fig. 7). We heard no songs from the 'Akikiki, only call notes, which resemble those of the Hawai'i Creeper (*Oreomystis mana*) but are a bit louder (Pratt 1992b). Since 1975, the 'Akikiki has declined catastrophically. A 1990 expedition to Sincock's Bog failed to find any (Pyle 1990), although subsequent searches have found them in the area in low numbers, even after Hurricane Iniki (Pyle 1993b). None were found by Walther (1995) in his 1994 surveys west of the Alaka'i Wilderness Preserve, although D. Kuhn (pers. comm.) and tour groups led by HDP have consistently found them through 1995 at the Kawaikoi Stream crossing on the Alaka'i



FIG. 7. Juvenile 'Akikiki (*Oreomystis bairdi*) showing distinctive white "spectacles," Alaka'i Swamp, 1975. Photos by RJS.

Swamp Trail, the most reliable locality outside the preserve (Pratt 1993). Recently, 'Akikiki have again been found in encouraging numbers along the Mohihi-Waiālae Trail (Pyle 1996). Appropriately, the 'Akikiki is being considered for listing as an Endangered Species (T. Pratt, pers. comm.).

As with other insectivorous Hawaiian honeycreepers, the classification of the 'Akikiki has been somewhat controversial. Pratt (1979) placed *Oreomystis* with the other thin-billed insectivores, excluding the enigmatic and possibly nondrepanidine (Pratt 1992a, Tarr and Fleischer 1995) *Paroreomyza*, in the tribe Hemignathini, but a cladistic analysis supported its independent derivation from a finch-like ancestor (Pratt 1992b). Johnson and co-workers (1989), whose analysis of drepanidine phylogeny substantially and irreconcilably disagreed with those of other biochemical systematists on many points, recommended that *Oreomystis* and *Paroreomyza* be placed in one tribe and all other drepanidines in another. Tarr and Fleischer (1995) found *Oreomystis* to be allied with the finchlike Psittirostrini and not closely related to *Paroreomyza*. We believe transfer of *Oreomystis* from the Hemignathini to the Psittirostrini is justified, even though it would become the only insectivorous genus in that assemblage, assuming Pratt's (1979) placement of the Maui Parrotbill (*Pseudonestor xanthophrys*) with the Hemignathini (contra AOU 1983) is correct. The question of whether *Oreomystis* is monotypic (Olson and James 1982, 1991) or includes the Hawai'i Creeper as *O. mana* (Pratt

1992b) will be discussed elsewhere (Pratt in press).

'Akeke'e (*Loxops caeruleirostris*), RK.— This species, formerly called Kaua'i 'Akepa, was common in the study area and provided daily observations, but none was singing at the time. They kept to the outer canopy where feeding movements were difficult to discern in detail. 'Akeke'e often appeared among inflorescences of 'ohi'a, but we could not confirm whether they actually took nectar. Subsequent research has revealed that the 'Akeke'e forages almost exclusively in 'ohi'a (Lepson and Pratt in press), unlike its sister species, the 'Akepa (*L. coccineus*), which forages in a wide variety of trees and shrubs (Pratt 1989b, Conant 1981, Lepson in press).

The bills of the two *Loxops*, with their slightly crossed tips, have been the subject of much speculation as to the manner of their use. Based solely on their study of the birds' strongly asymmetrical jaw musculature and skeleton, Richards and Bock (1973) presented a lengthy and highly detailed scenario of how the bill might be used. Both methods they described involve a 90° rotation of the head during feeding, a twisting motion that should be obvious to an observer, yet none of our observations in 1975 or subsequent ones of both species involved any such movement, nor has it been reported by any other observers. When foraging among leaf buds, both the 'Akeke'e and the 'Akepa look just like birds feeding at inflorescences, i.e., the head is held still and all action is accomplished by the bill and tongue. Benkman (1989) described the feeding of the 'Akeke'e at Pu'u o Kila in the Koke'e area in some detail: no head-twisting occurs; the bird parts the scales of 'ohi'a leaf buds by gaping and laterally abducting the lower mandible after the closed bill has been inserted. HDP confirmed Benkman's observations at the same locality in October 1992 and also observed the action of the tongue, which Benkman (1989) did not report. After the leaf scales were pushed apart, the tongue was extended vertically down into the crevice, then withdrawn into the bill with a small linear object (presumably an insect larva) entangled at a 90° angle in the brush-like tip. On 24 September 1995 HDP observed identical feeding movements by several 'Akeke'e in the upper Kawaikoi Stream valley along the

Alaka'i Swamp Trail. To date, no aspect of Richards and Bock's (1973) scenario has been confirmed by field observation.

In February 1993, HDP made an enigmatic observation of 'Akeke'e feeding behavior at the northern edge of the Alakai Wilderness Preserve: a male 'Akeke'e twice bit the edge of a mature 'ohi'a leaf, pinking the edge with two v-shaped indentations about 1 cm apart. The leaf could not be examined closely but through 10 × 40 binoculars appeared healthy and without any insect damage. Whether the bird ate the leaf sections could not be determined. Among HDP's 1995 observations were several "nibbles" at leaf edges, but no sections were removed. Folivory in general is very rare in birds (Munson and Robinson 1992) and has previously been reported in only one Hawaiian honeycreeper, the Laysan Finch (*Telespiza cantans*, Conant 1988).

'Apapane (*Himatione sanguinea*), *RE*.—This was the most common bird in our study area. Numerous adults and immatures were taking nectar from 'ohi'a flowers in the tree tops. Songs and call notes were given virtually all day. This was one of the two species that the Kaua'i 'O'o chased from a grove of heavily flowering 'ohi'a trees (probably the 'o'o's feeding territory). 'Apapane were abundant at Koke'e in 1975 and remain common today but were noticeably reduced by Hurricane Iniki. One seen in a ravine in Kalaheo, a lowland locality directly south of Sincock's Bog, by members of a tour group led by HDP six weeks after the storm provided modern confirmation of historical accounts of displacement of montane birds by storms (Pratt 1994a).

'I'iwi (*Vestiaria coccinea*), *RE*.—We saw this bird daily, but not frequently. Solitary individuals took nectar from 'ohi'a, *Clermontia* spp., and *Scaevola glabra*. We did not see it gleaning for insects amongst stems and foliage, as it may do when nectar is scarce. 'I'iwi, as well as 'Apapane were the target of feeding territory aggression by Kaua'i 'O'o. When taking nectar from flowers of *Clermontia* and *Scaevola*, 'I'iwi invariably pierced a hole in the base of the long tubular corollas characteristic of these plants. This feeding method contrasts with earlier observations such as that of Spieth (1966) and contravenes the seemingly obvious and often-cited evolu-

tionary relationship between the bills of Hawaiian honeycreepers and the flowers they feed upon (Givnish et al. 1995, Lammers 1995, Patterson 1995). It clearly amounts to nectar-robbing because the bird avoids contact with the flower pistil. This anomaly leads us to speculate that this habit may be a recently learned feeding behavior influenced by introduced flowers with flower structures that evolved with different pollinators. Similar behavioral modification has been reported among Australian nectarivores (McCulloch 1977). Henshaw (1902) observed that 'I'iwi on Hawai'i had learned to pierce the "spur" of nasturtiums to reach the nectar, and Perkins (1903) reported Hawai'i 'Amakihi feeding on long lobelioid flowers that "they have learnt to pierce at the base, at least in certain localities." The flowers of the introduced South American passionflower *Passiflora mollissima*, known locally as banana poka, are too long and too straight for the 'I'iwi's curved bill, so the birds must pierce the corolla at its base to reach the base, as we have frequently seen them do. When in heavy bloom, these choking vines attract large assemblages of birds with the 'I'iwi predominating. Other species that frequent banana poka include Kaua'i 'Amakihi, 'Anianiau, 'Apapane, and Japanese White-eye. Whether the smaller-billed species are capable of piercing the large and relatively tough banana poka corollas or simply take advantage of holes made by 'I'iwi is not known. Such feeding assemblages were conspicuous at Koke'e in 1975, but the alien plant had not yet penetrated the heart of the Alaka'i. Nevertheless, banana poka may have had an insidious impact even in areas remote from infestations. Many large flowers native to Hawaiian forests, including representatives of such disparate families as Campanulaceae (Givnish et al. 1995, Lammers 1995), Malvaceae (Funk and Wagner 1995), and Goodeniaceae (Patterson 1995) in which flowers are not usually curved, have curved corollas and other structural modifications for feeding, and presumably pollination, by native birds. By "teaching" birds to rob nectar without pollinating flowers, banana poka and other alien plants may have broken the evolutionary link between Hawaiian plants and their bird pollinators. Thus, alien plants could be damaging

native ecosystems in a particularly devious way.

The voice of the 'I'iwi is highly distinctive compared to those of other drepanidines. It includes metallic screeches, dissonant reedy notes, bell-like notes, clicks, and humanlike whistles delivered in a measured, seemingly random cadence quite unlike the canarylike songs of drepanidine finches and the simple warbles and trills of the Hemignathini. Other members of the Drepanidini, though they share some of the 'I'iwi's tonal qualities, have much more "conventional" songs. Remarkably, the 'I'iwi's song bears a strikingly close resemblance to portions of the song of the aforementioned New Zealand Tui (see Kaua'i 'O'o account). In fact, one could produce a reasonable facsimile of the Tui song by splicing together pieces of the songs of the 'I'iwi and the Kaua'i 'O'o! None of these songs are much like the songs of meliphagids of central Polynesia (*Foulehaio carunculata*, *Gymnomyza* spp.). Why the songs of two unrelated Hawaiian birds should resemble so closely that of a bird that lives thousands of kilometers away is fertile ground for speculation. One possible explanation is that the song of the 'I'iwi developed as a response to food territoriality by as yet unknown Hawaiian meliphagids.

Nutmeg Mannikin (*Lonchura punctulata*), A.—HDP saw three birds in Sincock's Bog on 8 July, having heard one calling earlier in the week. Although primarily found in lowland open habitats, Nutmeg Mannikins are commonly seen along trails in the Koke'e region and are the most likely of Kaua'i's introduced estrildids to be found in forest openings.

CONCLUSION

Our 1975 experience in the Alaka'i wilderness, viewed in two-decade hindsight, teaches several important lessons for biologists and environmentalists. Because it retained a relatively intact avifauna into the 1970s, biologists of the time were comparatively complacent with regard to both research and conservation on Kaua'i. Whereas Maui and Hawai'i were the subject of major research and conservation efforts in the 1970s, Kaua'i's forests held the long-term attention only of John Sincock, and it was the last of the islands to be surveyed systematically (Scott et al. 1986).

Although major preserves were established by the federal government and The Nature Conservancy of Hawaii in forests on Maui, Moloaka'i, and Hawai'i, Kaua'i saw only the belated designation of the Alaka'i Wilderness Preserve by the State of Hawaii. We cannot fault authorities for such actions; we, too, considered Kaua'i "safe" when compared to other islands that appeared to have more pressing concerns. The sudden collapse of Kaua'i's avifauna was a surprise. During the same period, Guam experienced an equally sudden ecological catastrophe that was also unexpected and rather mysterious (Pratt et al. 1979, Savidge 1987, Jaffe 1994). Neither island was perceived to be in imminent danger in the early 1970s, and both experiences show that island avifaunas can quite literally be here today, gone tomorrow. We now know that island avifaunas worldwide are mere remnants of what was present before the influence of humans (Olson 1989b; Steadman 1995), but these geologically rapid extinctions were slow compared to recent insular avian disasters. Any small-island endemic might well be considered inherently endangered. Although in the past HDP argued against listing locally common island endemics as Endangered Species (Pratt et al. 1979), we now believe that those who set conservation priorities should use different criteria for island versus continental species. That insularity, in and of itself, greatly increases any species' vulnerability can no longer be disputed.

We further believe that conservationists should revise their view of nominal island subspecies. Some conservationists (e.g., Hazevoet 1996) have suggested that the new "phylogenetic" species concept (Cracraft 1983), in which all distinctive island forms would be considered species, would better serve their purposes. However, such practical considerations are largely irrelevant to the ongoing philosophical debate in ornithology over species concepts (see Zink and McKittrick 1995 for a review). In our view, conservationists should work to save all distinctive island populations whatever species concept ornithologists ultimately adopt. We predict that most such populations will ultimately be shown to be good biological as well as phylogenetic species. In many cases, the requisite data necessary to shift the burden of

proof to the lumpers is available even in the original taxonomic revisions, which only need to be reinterpreted in the light of modern insight. In other cases, recent observations of vocalizations and ecology can help in the reassessment of species limits as we have done herein for several Kaua'i forms.

The "species only" policy of Collar et al. (1994), although understandable given the size of the problem, is unfortunate. The Kama'o, which was considered a subspecies of the 'Oma'o (*Myadestes obscurus*) until Pratt (1982) showed it to be a full biological species, is a case in point. By the time the new classification was officially adopted (AOU 1985), the population was so low that little could be done to save it. In 1975, biologists had far more concern for the Puaiohi, yet today the historically rarer thrush survives while the Kama'o apparently does not. A captive breeding program begun in 1975 might have gotten the species through the recent hurricanes, but none was even contemplated for a bird that was "only" a remote island subspecies.

Other conservation lessons from our observations include the findings that alien species on islands may have deleterious effects in previously unforeseen ways and that survival strategies that worked well in a pristine environment can become maladaptive in damaged ecosystems. Our studies also show that even seemingly superficial observations of island birds are important and should be published; we can never know when a given study may be the last. Most oceanic islands are much less frequently visited by ornithologists than Kaua'i. Gaps in the ornithological literature of 30 to 50 years are not uncommon for remote islands. Even a short interlude on a seldom-visited island can provide important data, and both scientists and recreational birders should neither overlook opportunities to make such observations nor denigrate the results as too superficial to be of value. Simply knowing whether a given species was present on a certain date may prove critical. Because islands are extremely useful natural laboratories for evolutionary and ecological studies, preservation of their avifaunas is particularly important and must be addressed immediately. Procrastination means extinction.

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